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Thesis

ON THE PHYLOGENETIC DEVELOPMENT OF CEPHALIZATION AMONG THE INVERTEBRATA

by

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ON THE PHYLOGENETIC DEVELOPMENT OF CEPHALIZATION AMONG THE INVERTEBRATA

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FOREWORD

In the following pages two major theories are involved some discussion of which is deemed necessary outside of the main portion of the text. These are (1) Clark's theory of zoögenesis[1]; (2) Child's theory of a physiological gradient of metabolism in animals.

The first of these has largely been disregarded. This is because of the following considerations: (1) I do not see that it makes much difference from our present viewpoint whether animals arose on separate evolutionary lines from the gastrula stage as Clark maintains or whether, on the other hand, the major phyla split off farther up on an evolutionary tree as postulated by the older theories. In either case the head developed in response to the same evolutionary forces, whether these forces are those postulated in the present paper or not. (2) I see nothing radically new in Clark's theory of evolution, that is, nothing which is fundamental. He has merely pushed back the branches of the phylogenetic tree so that they now arise nearer the base of the stem. Continuing the figure, Clark's tree would be more like a clump of trees arising from a common stem near the ground. The branches of these represent the classes, orders, and other taxonomic subdivisions.

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[1] See Clark, A.; Zoögenesis, 1930; Williams and Wilkins Co.

The second theory mentioned above has been tentatively accepted; this is because of the following. While it is recognized that Child's theory is still a theory, it is also to be noted that it may be substantially correct. The theory fits in beautifully with the viewpoint put forth in the present paper and, if proved true, will do much to substantiate what is said here. On the other hand, if further observations show Child to be wholly wrong, the ideas of cephalization and its development put forward here will not be seriously affected.

Throughout this paper I am dealing with matters upon which for lack of knowledge no two zoologists are likely to agree entirely. In treading such hypothetical ground certain theories must of necessity be tentatively accepted and others rejected. Which should be taken and which should be discarded is largely a matter of opinion.

ON THE PHYLOGENETIC DEVELOPMENT OF CEPHALIZATION AMONG THE INVERTEBRATA.

The importance of the differentiation of a morphologically distinct head in the phylogeny of the vertebrate animals is generally recognized. The head, as a morphologically distinct structure, contains the principal nerve center (the brain), the more important sense organs such as those of vision, hearing, taste, and smell and the oral cavity with all of its attending structures as well as the principal intake apparatus for securing the all important oxygen so necessary for life. In fact, so far has the morphological differentiation of the head gone in the vertebrates in general that, even in the most primitive of them, this structural feature deals directly or indirectly with most of the primary functions of the body. Sense perception (except for that of touch and a few other minor senses such as those connected with the lateral line of fishes), the correlating functions of the nervous system, the intake of food and of oxygen, many mechanisms of defense (as where teeth, tusks, or fangs have been developed), and most mechanisms for balance, for associative memory, and, in the higher forms, for those phenomena known subjectively as will, reason, and the various instincts are all localized in or associated with the head.

It is generally recognized, too, that the vertebrate animals arose from some primitive stock among the inverte-

brate phyla. Whether the primitive ancestor of vertebrates was an arachnid as Patten has recently maintained, an annelid-like worm which gradually reversed its position, or an animal somewhere midway between the larval tunicate and the present day Branchiostoma is immaterial to our discussion. Whichever of these is true (if, indeed, any of them is) it is well established that the vertebrate organization is of an advanced type. It follows from this, logically, that the invertebrate animals must have arisen first in phylogeny; and paleological evidence bears this out.

Since vertebrates arose from some invertebrate stock, and since the head has become in these a very important structural and functional feature, it seems strange that no one has looked to the recent invertebrates with the idea of tracing the development of the head. How and where did the head arise? Where in the invertebrate series may we see its beginnings? What features of environment have tended toward its development in some groups and its suppression in others? These are questions which need to be answered.

It is the purpose of the present paper to review the main structural features of the various invertebrate phyla so far as they deal with the head, considering each in its proper relation to adaptation to the normal environment of the animals in question, that is, to the normal activities of the animals in their usual environment.

We shall attempt to show that there has been a steady progression in the development of a head among the inverte-

brate animals but that, as might be expected, several phyla have remained relatively primitive in this respect.

Few if any new factual data are to be presented. Rather, this is a review of old facts, many of them very well known, from a new viewpoint. Method of organization and application of well-known knowledge to a relatively new idea constitute the only basis of originality claimed.

Let us begin by defining several special terms used in the discussion.

1. Cephalization. This term has been used (for the vertebrates) to mean the phylogenetic development of a head end, with special reference to the amassing of nervous material in this region. For the invertebrates, the entomologists have used it to mean the phylogenetic fusing of ganglia of the central nervous system such as is found in some of the higher Diptera where the abdominal ganglia primitively present have disappeared leaving three large nerve centers, the superoesophageal, the suboesophageal, and a large thoracic ganglion. For the present paper we shall extend the meaning somewhat and use it to indicate any development of a morphologically or physiologically distinct end of the body which tends to go ahead in normal progression, especially if the mouth and principal nerve centers and sense organs are developed thereon. I shall also use the term to express any

distinct tendency in this direction.

2. Primitive. I shall use this term with reference to any animal, anatomical part, or physiological process which we consider as phylogenetically old --- that is, one which has not changed much during evolution.

3. Specialized. I shall use this in opposition to primitive --- that is, anything which is phylogenetically young or which has arisen through evolutionary development from a more primitive condition. Both of these terms, primitive and specialized, are, of course, relative terms, used to express different degrees of the same phenomenon. For example, Paramecium may be considered a primitive animal in that it has retained a unicellular organization; but it is by no means a primitive protozoon since it is seen to have many specialized parts when compared with the more primitive Amoeba.

4. Generalized. I apply this term to any animal, anatomical part, or physiological process which can become changed through further evolutionary development or which has not yet become adapted to any one function. It follows that any generalized biological structure or process is, in the nature of things, primitive.

5. Degenerate. This term has been much misunderstood. It refers to animals or anatomical structures which

have lost parts which ancestors had. It follows from this that degenerate animals or structures are always specialized. A tapeworm, for example, is a degenerate animal in that it has lost all vestiges of a digestive tract --- but this is a specialization in adaptive response to parasitic life. Degeneration, therefore, is but a type of specialization. This is often forgotten in discussions.

The promophology of animals also has a distinct bearing on our subject. There are four conditions of symmetry among animals. These are; (1) asymmetry, (2) radial symmetry, (3) bilateral symmetry, and (4) conditions intermediate between some of these.

Asymmetry is manifested by relatively few animals --- mostly by some of the amoeboid Protozoa. In these (e.g., Amoeba, Endamoeba, Valkamphia, etc.) there are no permanent axes around which the structures of the body are placed. Because of this, many asymmetrical animals may take on a temporary condition suggestive of bilateral or radiate forms. Thus, Amoeba proteus when progressing in a single direction for some time with the whole body acting like a single pseudopod may appear temporarily quite like a bilaterally symmetrical type; and A. limax, Pelomyxa palustris, and others are almost permanently in this condition. Similarly, whenever an Amoeba proteus loses its contact with the substratum, without which it cannot progress, it sends numerous, long, extremely slim pseudopodia in all directions as if to

seek contact. Under these conditions the animal appears distinctly radiate.

Radial symmetry is found among several widely separated taxonomic groups. It is manifested by certain of the Protozoa, all Porifera (although excessive budding often masks it), all Coelenterata, and typical Echinodermata. The fundamental characteristic of this type of promorphological organization is that a varying number of axes radiate into the same of different planes from a common center. Around these the parts of the body are symmetrically placed, each radius thereby having the same type of organs in the same relative positions as any other. Organs of which there is but one of a type are typically placed at or near the center.

Bilateral symmetry is manifested by most other animals. It is characterized by having a single plane, containing the longitudinal axis, which divides the body into right and left halves one of which is the mirror image of the other. All organs of which there is but one of a type lie in the longitudinal axis; all paired organs are disposed one of each pair on each side of this axis. Thus, the body always shows right and left sides, distinct dorsal and ventral surfaces, and anterior and posterior ends.

Some authorities recognize another type of organization known as spherical symmetry in which the body is spherical or spheroid and without radiating axes. We consider this but a type of radiate organization.

Intermediate conditions will be illustrated later.

In discussing the beginnings of cephalization as manifested by the lower invertebrates, one should first note what characteristics indicate these beginnings. These are: (1) having one end of the body more sensitive than the other; (2) possessing a higher rate of metabolism at one end (i.e., having a metabolic gradient); (3) having a definite bilateral symmetry or, at least, a tendency toward it; (4) having the principle nerve center or centers nearer one end of the body than the other; (5) having a tendency for the mouth to be near one end of the body; (6) having organs of special sense such as those for perception of light and sound associated with one end of the body more than with the other; and (7) having a tendency for one end (especially the one manifesting other tendencies toward cephalization) to go ahead in normal progression. Any animal possessing any one of these characteristics has some degree of cephalization. The interrelations of these characteristics are such, however, that even the most primitive forms showing the condition at all typically manifest several of them and, in morphological types having a high degree of cephalization, all of these characteristics are developed to a high degree. Occasionally, however, other evolutionary tendencies have tended to mask one or more of them as in the case of the human which, because of the change of function of the pectoral limbs and the consequent adoption of bipedal locomotion, now carries the ventral surface rather than the anterior end ahead; tendencies in this same direction are also seen in other Primates,

notably the gibbons, and in some birds.

Let us now examine the various phyla of invertebrate animals to ascertain what degree of cephalization each morphological type shows at the present time.

CEPHALIZATION AMONG THE PROTOZOA

A true head has never been developed among Protozoa in the sense that one has developed in the arthropods and vertebrates. Amoeba and its allies (Pelomyxa, Valkamphia, Sappinia, etc.) of the order Amoebina, as well as the trophozoites of some of the Sporozoa, move about in any direction carrying one end temporarily ahead. No morphological structures are more closely related to one end than to the other.

However, these forms do show the very slightest degree of incipient cephalization. The part acting as the temporary anterior is slightly more sensitive to strong stimuli than are other portions. How slight this tendency is, however, is shown by the fact that any portion of the body surface may become anterior and thus show greater sensitivity. No one portion of the body surface has become fixed to form a permanent anterior end.

From another viewpoint, one could logically maintain that no cephalization whatever is manifested by these animals.

Other orders of Sarcodina are principally radiate in organization. Thus Actinosphaerium, Actinophrys, Radiophrys, Clathrina, and other Heliozoa are essentially spherical organisms with long thin pseudopodia radiating in all direc-

tions from a common center. Locomotion is rare in these forms. They are typically free-floating, depending upon chance currents for movement from place to place. No part of the ectosarc is more sensitive than other parts and no part tends even temporarily to go ahead. The same in essence may be said of the Radiolaria and Foraminifera. None of these animals show the slightest tendency toward cephalization.

In the Testacea we meet a slightly different condition. Arcella is an essentially radiate animal modified for living in a secreted shell. Pseudopods are protruded through the single "oral" aperture to be used for locomotion and food capture. The locomotion is essentially like that of an Amoeba, any one pseudopod temporarily anterior and probably more sensitive than other portions of the body. In Centropyxis, the aperture of the shell is placed nearer one edge and the whole test in this region has become flattened. While pseudopodia protruding through the shell mouth can extend in all directions as soon as they pass outside the test, the tendency is for the animal to move in one direction more than in others. This superimposes a sort of pseudo-bilateral symmetry upon a theoretically radiate animal. This is, therefore, a case of a condition intermediate between bilaterality and radiality. In so far as this and related genera show bilateral symmetry, they also show cephalization. We shall meet this very condition again among the echinoderms known as Clypeastroidea, Spatangoidea, and Holothuroidea. In Difflugia and its closest relatives there is yet another

condition. The shell is urn-shaped and is carried bottom-side up over the amoeboid body. Pseudopodia protrude through shell mouth and may radiate in all directions, provided that the shell be carried upright. In this condition the protozoon suggests a tiny octopus in appearance and manifests little or no cephalization. However, often the heavy test sags toward one side and the pseudopods then all or nearly all extend in the opposite direction, locomotion accordingly being wholly in this direction. Under these conditions the organism still suggests an octopus but one with the heavy body lying toward one end and all of the arms (represented by pseudopods) extending in the other direction.

If we compare Arcella, Centropyxis, and Difflugia we note a progressive cephalization, nowhere marked, among them. Arcella is almost a typical radiate form, its shell being like a tiny derby hat with the shell aperture in the exact center of the lower surface. Centropyxis has the test mouth moved to one side and the shell in this region modified. Furthermore, the animal tends to move in locomotion in the direction indicated by the modified shell more than in other directions although still capable of movement in all directions. In some species the shell has lengthened slightly so that anterior and posterior ends tend to be distinguishable. Furthermore, the under surface of the test is flattened somewhat thereby suggesting a ventral surface. This surface is always carried downward in normal progression. In Difflugia, the test is further elongated, especially in

certain species, but the shell is not flattened. In the lengthening of the shell, this genus is more specialized than either of the others in the direction of cephalization. In failing to have developed a ventral surface, however, it is more primitive than Centropyxis.

In the flagellate group, practically all genera are differentiated in such fashion as to have anterior and posterior ends, the flagella typically arising near the nucleus and leaving the cell at or near the anterior as in Euglena, Phacus, and Chilomonas. Many of them have a cytostome also, at the anterior end, although green forms like Euglena seldom if ever take in solid food. Saprozoic forms like Chilomonas are similar in that the cytostome is not used for ingestion; but a portion of the anterior end is modified for absorption of dissolved food materials from the surrounding medium. A stigma at the anterior end is characterictic of Mastigophora, especially of pigmented forms like Euglena, Eudorina, Pandorina, various other monads, and Volvox. This is supposed to be more sensitive to light than the remainder of the body. If this be correct, we have in it the first manifestation of a morphologically distinct sensory structure at the anterior end of an organism. This would be, then, the very beginning of cephalization based upon such structures. It will of course be understood that in saying this I am not implying distinct nervous organization to these unicellular organisms. The stigma is not an organ but, rather, an organelle.

The colonial flagellates like Volvox and Gonium present an interesting picture. Each somatic cell of Volvox, for example, is differentiated into anterior and posterior ends from the former of which two flagella protrude. Each has a stigma near the anterior end much as has Euglena. However, this end does not go ahead in progression; another evolutionary tendency has modified this expression of cephalization.

This other factor is associated with the colonial form of organization. Each somatic cell of the colony is organically joined to several surrounding cells by cytoplasmic bridges. As is usually the case in such circumstances, the union of cells is physiological as well as morphological. Through the bridges of cytoplasm some sort of impulses pass so that, when locomotion takes place, the movement of the individuals is coördinated so that the colony as a whole moves in a single direction. The result is that, while each cell manifests the amount of cephalization characteristic of the flagellate class, the colony is built on a radiate plan --- it moves as freely in any one direction as in any other.

The germ cells of Volvox, whether micro- or macrogametes, act singly and therefore show the same degree of cephalization that would be expected of typical flagellates.

Dorsal and ventral surfaces and right and left sides are not usually differentiated in the Mastigophora. However, there is one case of striking bilateral symmetry. Giardia,

an endozoic mastigophoran genus with species in the digestive tract of man and other mammals, is definitely bilateral with distinct dorsal and ventral surfaces and with flagella symmetrically placed on each side.

The flagellate group as a whole shows a greater cephalization than does the Sarcodina. This is probably correlated with their method of locomotion, a fact indicated by the flagellated isogametes produced in several species of amoeboid Protozoa. These gametes are relatively long and slim, having the typical organization of a mastigophoran although belonging to the Sarcodina. In all such cases, even though the adults manifest little or no cephalization, their gametes do so. This may indicate that bilateral symmetry is more primitive than radial symmetry or asymmetry; more likely it means simply that dispersal is better served by flagellate locomotion than by amoeboid. Incidentally, we perhaps should mention that some flagellates have amoeboid gametes.

The Sporozoa are so specialized for parasitic life that little cephalization is manifested in the group. About the only suggestion of it which occurs, other than that which has already been mentioned, is in the Gregerinida whose bodies are differentiated into two portions which might be considered anterior and posterior. Since, however, the adults do not move from place to place, these differentiated ends cannot certainly be said to be of this nature; the "anterior" may be only for the attachment to the host and not

a true anterior at all.

The Infusoria are the most differentiated of Protozoa in many ways and, as might be expected, it is in this group that cephalization among Protozoa is best shown. These animals show two types of organization expressed taxonomically by dividing the class into the Suctoria and Ciliata. The former are largely passive as adults and typically show asymmetry or are radiate forms floating in water in much the same manner as the Heliozoa already discussed. Their "embryos" are much like the Ciliata which are discussed below.

It is plain from the above that it is the Ciliata which show the greatest degree of cephalization to be found among the Protozoa. While there are exceptions in various degrees in this group, most Ciliata are differentiated into distinct anterior and posterior ends and they may have recognizable dorsal and ventral surfaces. Beginning with Haltaria (Order Oligotricha) we may trace cephalization through various stages of manifestation to the highly organized members of the class which have not only dorsal and ventral, anterior and posterior, and lateral portions distinct but also have a mototorium (corresponding physiologically with a nerve center) with cytoplasmic fibrils (specialized for conduction of impulses much like nerves) for correlating the various activities of the body. This is seen, for example, in the common Paramecium caudatum.

Haltaria is nearly spherical. Few cilia and many spines protrude from its body into the surrounding medium.

It is very erratic in movement, darting this way and that and with no end going constantly ahead in progression. Some other oligotrichs, however, have become elongated along the longitudinal axis and, therefore, show incipient cephalization.

In the Peritricha (Vorticella and its allies) we have an interesting condition. When feeding, all of the common Vorticellidae sit upon stalks and waft food particles toward themselves by creating powerful currents in the water by means of long peribuccal cilia. The body is formed like a bell and cilia occur only on the outer margin and in the cytopharynx. The cytostome opens from the oral disc and the cilia in this region are fused to form membranelles, the better to serve for food capture. Some genera are colonial, many individuals occupying a common stalk (Carchesium and Epistylis); others are non-colonial (Vorticella). A single vorticellid when in this condition clearly manifests radial symmetry --- in fact it strikingly suggests a coelenterate polyp in general appearance. Colonial forms similarly suggest colonial genera of Hydrozoa such as Campanularia or Obelia.

The only suggestion of cephalization which such an organism shows is that its oral surface is more sensitive than other portions of the body. If, as often happens when vorticellids are feeding, the currents created by the peribuccal cilia swing a diatom or other relatively large object forcibly against this end, the organism recoils sharply. The peristome contracts and the whole animal becomes spheroid. Stimulation on the side of the animal will also cause this

reaction but it takes less stimulation on the peristomial disc than elsewhere to produce the effect. Vorticella, when stimulated in the manner indicated above, springs backward by violently contracting the spasmoneme within the stalk. Colonial forms either have no contractile stalk or else the major or common stalk contracts when one organism is stimulated. In these latter forms, therefore, there is a physiological as well as a morphological union; some sort of impulse (which in higher animals we should call neuroid transmission) is passed between individuals.

Occasionally, when food is becoming scarce, and commonly, when the chemical condition of the environment is poor, Vorticella breaks from its stalk and swims about. Its body loses the typical bell-like shape and would then hardly be recognized by its general appearance as the same organism. This condition is also seen normally upon division of the animal. One daughter cell retains the old stalk; the other swims away to settle in another spot and form a stalk of its own.

When thus free-swimming, Vorticella manifests a certain degree of cephalization. It carries its sensitive oral surface ahead and acts much like a bilaterally symmetrical type upon stimulation. As we shall see later, these phenomena are also shown by Stentor (Order Heterotricha).

The difference in behavior of Vorticella under the varying conditions cited above serves to illustrate a general principle having rich application throughout living things.

Radiate animals are typically sessil in habit or are very slow in locomotion; bilateral animals, relatively active and fast. In fact, so close is the correlation between a sessil habit on the one hand, and radiate organization on the other, that we see ample expression of this principle in the plant kingdom as well as among the animals. Practically all of the higher plants (Spermatophyta) are radiate --- and all are sessil. Even Bryophyta and Pterydophyta show this tendency but the Thallophyta are so low and primitive in general organization that no promorphological organizational pattern has become fixed for the group.

This principle that active animals tend to be bilateral (or, put in another way, that bilaterality allows for greater activity) has a distinct bearing upon the problem of cephalization. Radiate organisms cannot, in the nature of things, have a true head; and sessil organisms do not in general develop one. When they have done so, they have often tended to lose it again in response to new conditions. We shall see several examples of this later in multicellular forms.

It follows from the above that true cephalization can be manifested by bilateral forms only. They are the only forms which can centralize nerve centers with attending sense organs (or their analogues in the case of unicellular forms) at one end; it is only they which can carry this important end ahead in normal progression; and it is only they which ordinarily can manifest a true metabolic gradient --- living

faster, as it were, anteriorly and progressively less so posteriorly. This will be further discussed later.

Returning to Vorticella, we note in this organism about as much cephalization as can be manifested by a radiate animal. Its peculiar interest lies in the fact that its radiate organization seems to shift toward bilaterality under certain conditions.

In the Hererotricha, two types of organization are evident, the one represented by Stentor, the other by Blepherisma and Spirostomum. The first of these animals behaves much as does Vorticella and illustrates the same principles so we need to discuss it no further.

Blepherisma and Spirostomum, especially the latter, are elongate. Each has a distinct anterior and a distinct posterior end as well as dorsal and ventral surfaces. The cytostome in these forms has shifted its position towards the posterior along the ventral surface so that it opens into the cell at some distance from the anterior end. The path taken in the phylogenetic migration of the mouth is indicated by a deep groove (the buccal groove) extending caudad from the anterior tip of the body. This groove is differentiated into a very efficient apparatus for the intake of food, being supplied with numerous long cilia some of which have fused to form membranellae, especially in the cytopharynx just inside the mouth.

In having morphologically distinct anterior and posterior ends and dorsal and ventral surfaces, these organisms

show some cephalization. Whether the anterior end is most sensitive to stimulation or not has not been definitely shown for these forms but it would be very surprising if this were not the case. Stentor, belonging th the same order and having much in common with Blephrisma and Spirostomum, has been shown to have a very sensitive oral disc, capable even of selection of food.

The Holotricha are much like Blepherisma and Spirostomum in their manifestation of cephalization. Typically, they have anterior and posterior ends which are recognizable as such. Whether they also show dorsal and ventral surfaces depends largely upon the extent of the phylogenetic migration of the cytostome in specific instances.

Some endozoic species have no mouth (Opalina ranarum, for example). Coleps and Didinium illustrate types with the cytostome at the anterior end. The latter has the anterior end quite well differentiated for the intake of food, there being a conical proboscis through the end of which the mouth opens and, located just inside the body proper, a system of rods for the strengthening of the cytopharynx. Coleps and Didinium, therefore, show very little differentiation of dorsal surface and ventral although the former is flattened a little on one side. Frontonia, Colpoda, and Colpidium each has a small mouth very near the anterior end, thus suggesting the early beginnings of cytostome migration with the attending differentiation of surfaces. The extreme is reached in Paramecium in which the cytostome has migrated so far backward that the

buccal groove extends over two thirds the length of the animal (except in one species where its extent is about one half) and the mouth opens into the cell very far toward the posterior.

Paramecium (especially P. caudatum) has been used more than any other protozoon to show that the anterior end is the more sensitive. After citing several experiments which show this in this genus and in Oxytricha (Order Hypotricha) and stating that the general results hold for many other Infusoria, Jennings[1] says:

> "Experiments of the kind just described have shown that the anterior end is as a rule much more sensitive than the remainder of the body surface. A light touch, having no effect at the posterior end, produces a strong reaction when applied to the anterior end".

Anyone having even a superficial knowledge of the ciliates will recognize the essential truth of this statement.

Paramecium illustrates another tendency toward cephalization found in several of the ciliates and mentioned in another connection earlier. A large mass of differentiated cytoplasm occurs which has been termed the mototorium. From this numerous fine fibrillae extend to all parts of the body. Experimental results show this system to function as

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[1] Jennings, H. S., 1931; Behavior of the Lower Organisms, p. 117; Columbia University Press.

a coördinator in locomotion and other body movements, from which the whole system consisting of the mototorium and fribillae is called the neurolocomotor apparatus. The discovery of this structure is a relatively new development in protozoology and, accordingly, it has been found in relatively few ciliates. Undoubtedly many more of them will be later shown to have similar structures as research develops.

The position of the mototorium in the body of Paramecium is interesting. It is toward the anterior portion of the cell and nearer to the ventral than to the dorsal surface. Its anatomical position, when correlated with its experimentally proved coördinating function, certainly suggests an analogue of a central nerve center of Metazoa. As such it shows considerable cephalization. Incidently, it also indicates that the ciliated unicellular animals are not primitive Protozoa and not even very primitive animals as is commonly taught, but rather that they are very specialized in their organization.

In many respects, the Hypotricha are the most specilized of Protozoa --- especially of free-living forms. Stylonichia, Oxytricha, and Euplotes may be taken as examples. Each of these forms has very distinct anterior and posterior, dorsal and ventral, and,in addition, lateral portions. The body is depressed and the cilia on the ventral surface have fused in many places to form large cirri, especially well developed in Euplotes, which are used much as a higher animal

(e.g., an insect) uses legs in one type of locomotion. They are very common in infusions where they can be seen quickly darting about or crawling over debris or algae in search of food.

Stylonichia and Oxytricha are among the ciliates mentioned specifically by Jennings (loco citato) as having especially sensitive anterior ends. Observation of Euplotes or almost any other member of this order will convince any one in a very few minutes that this is generally true in other forms. Some of the Hypotricha (e.g., Oxytricha) have also been shown to have a neurolocomotor apparatus.

SUMMARY OF THE BEGINNINGS OF CEPHALIZATION.

Taking the Protozoa as a whole, we observe the following opposing sets of principles concerning the beginnings of cephalization as exemplified by this phylum:

(1). No protozoon has a true head.

(2). Few Protozoa are truly bilaterally symmetrical.

(3). Some whole groups (e.g., Heliozoa, Radiolaria, and Suctoria) are fundamentally radiate and, therefore, manifest little or no cephalization either as a fact or as a tendency.

On the other hand:

(1). Most free-living forms (especially among the ciliates and flagellates) have differentiated sensitive anterior ends distinct in this respect from a less sensitive posterior in each

case.

(2). Two families (Vorticellidae and Stentoridae) are intermediate between radiate and bilateral forms.

(3). Many Protozoa have developed recognizable dorsal and ventral surfaces (e.g., Paramecium and all of the Hypotricha), so far developed in some (e.g., Giardia and the hypotrichs) as to show distinct right and left.

(4). Sensory structures and coördinading centers, when they occur, tend to be located toward the anterior and ventral more than elsewhere (e.g., stigmata of the flagellates and the neurolocomotor apparatus of the ciliates).

Putting these two sets of facts together we derive the following general statement: concerning incipient cephalization, the Protozoa vary widely; radiate forms have little or no tendency in this direction, bilateral forms (or those with incipient bilaterality) express cephalization in varying degrees. This is, after all, but an expression of the principle earlier stated --- that a sedentary life is clearly correlated with radiate promorphological organization and that bilaterality allows for greater freedom of movement.

CEPHALIZATION AMONG PORIFERA

Being essentially radiate in organization, the Porifera show little cephalization as adults. Their larvae, however,

suggest typical holotrichous ciliates in this respect. The simplest type of sponge larva (e.g., that of Clathrina blanca) is essentially a flagellated blastula and is known as a parenchymula.

This larva is differentiated into two poles, with two larger cells lying at one of them. All of the other cells are flagellated and alike. The end of the body opposite the one containing the two non-flagellated cells goes ahead in progression and, therefore, may be looked upon as anterior. This is about the extent to which cephalization is manifested in sponges, since more differentiated poriferan larvae (e.g., the amphiblastula) show essentially the same condition as far as cephalization is concerned.

CEPHALIZATION AMONG COELENTERATA

The symmetry of Coelenterata is radial and, in habits, these animals are largely sessil. There are some polyps which are motile, however, and most medusoid forms can actively swim.

Considering the polyps first, we may take Hydra as a typical example of a hydroid form which has considerable power of locomotion. The body of this organism is differentiated into two poles, the foot or base at one and the mouth at the other; these are known as the aboral and oral poles, respectively. The oral surface is differentiated somewhat and is much more sensitive than the aboral. Furthermore, regeneration takes place more readily at the oral end than at the other.

In many other Hydrozoa (sessil forms) Chicago scientists have shown a metabolic gradient extending from the oral end to the aboral. The fact that regeneration is more marked at the oral end of Hydra indicates that this is probably true for this form, also.

Considering these facts, one could interpret them to mean that the oral surface of Hydra is the beginning of an anterior end: but there is little tendency for this surface to go ahead in progression. When a Hydra moves from one place to another, it does it by one of four methods: (1) it slides on its base; (2) it somersaults; (3) it moves like a larval geomedrid; or (4) it attaches its tentacles, detaches its base, contracts the tentacles, and reattaches its base in a new region. The last method is known for Pelmatohydra oligactis (Schulze) only but probably is used by other long-tentacled species as well. The free-moving actinozoan polyps (like the common Metridium) move from place to place very little and, when they do, they tend to slide on their bases. Thus, the polyps do not carry the oral surface ahead in progression and, from this viewpoint, do not manifest cephalization.

The medusae of both Hydrozoa and Scyphozoa swim freely in the surrounding medium. But they carry the aboral surface ahead. Furthermore, their sense organs (otocysts, tentaculocysts, etc.) tend to be localized about the margin of the bell at the ends of some of the radial canals --- not, as one might expect, on the sensitive oral surface, nor yet

on the aboral surface which, in these animals, goes ahead in progression.

From the above it is evident that there is a contradiction in tendencies in the Coelenterata. The possession of a metabolic gradient and of a more sensitive oral surface indicates a certain degree of cephalic development. The facts that the more sensitive surface does not go ahead in progression and that the sense organs of medusae occupy neither oral nor aboral surface, however, indicate the reverse.

For these reasons, it seems best to interpret the oral regions of coelenterate polyps (and similar regions of medusae, when they occur) as comparable to the corresponding regions in the Vorticellidae. Both types of animals, although one is a protozoon and the other a coelenterate, have developed a special sensitive region about the mouth, the better to secure food.

CEPHALIZATION AMONG CTENOPHORA

The comb-jellies are also fundamentally radiate in organization. But, by a lengthening of the body in the axis between oral and aboral poles, and by the development of symmetrically placed tentacular pouches on each side of the body in most of them, they have had a superficial bilateral symmetry superimposed upon the fundamentally radiate body. Not only is this true but also the oral end is normally carried ahead in progression. Whether this end is the more sensitive to stimulation or not, I do not believe has been

definitely determined --- it would not be surprising if it were more sensitive.

On the other hand, the nervous system is diffused as in coelenterates, there being no special nerve center, and the principal sense organ is aboral in position --- exactly opposite the mouth. Dorsal and ventral surfaces are not differentiated from one another.

This indicates, as among the other lower Metazoa already considered, that whatever cephalization has started is very weak.

Up to this point we have been considering those animals which either show no cephalization at all or show it only in its incipiency. We now turn to those in which this phenomenon is more and more marked --- but we shall still find, here and there, an exceptional group which has become specialized in other directions because of special habits and habitats.

CEPHALIZATION AMONG PLATYHELMINTHES

The Platyhelminthes are the first animals to show cephalization clearly. In general, they manifest this through; (1) having a distinct bilateral symmetry, (2) carrying the anterior ahead in progression, (3) having a metabolic gradient, (4) having a nervous system consisting of ganglia in the anterior region and nerve cords running therefrom, (5) having sense organs in the anterior region associated with the cephalic ganglia, and (6) having a much greater sensitivity in the anterior region of the body. Some of them also

have the mouth anterior in position but others have a special condition, the mouth being far back and opening on the ventral surface. One class, the Cestoda, have no mouth, nor, indeed, any digestive organs, having lost these through degenerate specialization in adaptive response to endozoic life. Let us now look at each of these characteristics a little more closely.

(1). Distinct bilateral symmetry is shown by all Turbellaria, especially by the orders Tricladida and Rhabdocoelida. Of the former, Planaria may be taken as a typical example. The digestive organs consist essentially of a pharynx, and an anterior intestinal diverticulum, each of which is along the logitudinal axis of the body; two posterior intestinal diverticula, symmetrically placed on each side of the median axis; and many secondary diverticula extending from all portions of the primary intestinal divisions. The secondary intestinal evaginations are roughly paired, that is, there are approximately the same number on each side of the body so that when one looks at the body rather quickly and uncritically, its two sides appear alike in this respect. The nervous system consists of two ganglia, close together and somewhat fused in the midline, from each of which a nerve cord passes backward giving off branchas. Between the primary cords, various connecting nerve strands run, thus giving the whole the appearance of a ladder. Reproductive and excretory organs are similarly either paired or lie in or near the median sagittal plane. The Trematoda show essential-

ly the same condition although details of course differ somewhat. Among Cestoda, each proglottid is essentially bilateral although the whole animal has become so modified in many ways in response to parasitic life as to be somewhat exceptional.

(2). All of the Turbellaria and Trematoda carry the anterior end ahead in progression, both as adults and as larvae. The miracidium of Trematoda, for example, although tiny and relatively undeveloped, has distinct anterior and posterior ends both morphologically and physiologically. A few types (e.g., Vortex veridis and Convoluta paradoxica) among the Turbellaria have become much modified for symbiotic life, one expression of which is relatively little locomotion. When these forms do move, however, they carry that portion of the body which their contained structures would lead us to believe anterior ahead. The Cestoda move about very little as adults unless greatly stimulated, as when artificially removed from the host, and little is definitely known as to which end goes ahead when they do. These worms are so degenerate, however, that even though they did not move at all the fundamental idea that the Platyhelminthes normally carry one end ahead in progression would scarcely be affected.

(3). A distinct metabolic gradient was first shown in Planaria. Whether Trematoda and Cestoda also manifest one is not known. On theoretical grounds, one might expect this condition to exist in Trematoda but it would not be strange if this were not shown by the tapeworms.

From the viewpoint of the theory of cephalization

the presence of a metabolic gradient is of peculiar significance. One might expect the various life processes to be fastest at an incipient anterior end. This end, going ahead in progression, must be the exploratory portion --- it is the first to come into contact with danger and also with food. We should, therefore, expect this end to be speeded up by whatever forces effect phylogeny to conform to the necessity of coping with the ever-changing environment.

Correlated with this are, of course, (4) the tendency to develop important nerve centers with (5) their attending sense organs in this region and (6) the tendency for this end to be or become the most sensitive. Apparently, of these last three (4), (5), and (6), increased sensitivity tends to develop first in phylogeny, since it is found in many Protozoa which do not show even a tendency as yet toward the others.

We may see, with the flatworms as our principal illustration, a gradual beginning of a true head for the first time in the animal series. From the facts available, we may reconstruct this development somewhat as follows: (1) development of bilaterality tends to carry one end ahead; (2) this end, being more and more an exploratory region, develops greater sensitivity; (3) this necessitates corresponding metabolic adjustments, and a metabolic gradient becomes established; (4) In response to the same forces, the principal nerve center tends to develop there; and (5) increased sensitivity of the whole anterior end, gradually tends to become

fixed into a few organs of special sense, shown in Planaria by two pigmented eye-spots on the dorsal surface of the head and in many other Turbellaria by several pairs of them.

The Platyhelminthes, therefore, constitute the most important and most interesting group so far discussed. In them we see for the first time expressed together, six of the seven categories listed earlier as indicative of cephalization. Furthermore, most of these are in relatively incipient form. The seventh category, that of having the mouth anterior, is manifested by the Acoela and a few other Turbellaria and by all of the Trematoda. Therefore, this characteristic of cephalization is amply expressed by the group as a whole although not characteristic of them.

The first clear manifestation of cephalization is thus shown by the Platyhelminthes, especially by Turbellaria. Trematoda show it less distinctly and Cestoda still less. That the two higher classes are simpler in this respect than the Turbellaria indicates nothing except that both of them have evolved along the line of degeneracy. This is especially notable in Cestoda.

CEPHALIZATION AMONG THE NEMATODA

The Nematoda are highly specialized animals as the late Dr. N. A. Cobb has shown and not simple and primitive organisms as is commonly to be inferred from textbook statements. As such, they show considerable cephalization. From our viewpoint, they divide naturally into two groups, the

first free-living, the second parasitic. Many of the latter are so modified for endozoic life that we consider the former rather than the parasitic species to express the fundamentals of nematode structure.

The free-living nemas express cephalization in the following manners: (1) they are bilaterally symmetrical; (2) the principal nerve center (the circumoesophageal nerve ring) is always located in the anterior half of the body although it cannot be said to be definitely in the head; (3) the mouth is anterior; in many, slightly ventral also; (4) special sense organs on the anterior end are highly characteristic (e.g., amphids, palps, and, in some, well-developed eyes --- so well differentiated in a few as to have lenses; and (5) the anterior goes ahead in progression.

Endozoic species have most of these characteristics also but sense organs are not so well developed. They never have eyes and their amphids are small or lacking but the oral palpi are at least as differentiated, on the whole, as are those of free-living species.

The nematodes are thus seen to show a fair degree of cephalization. They have advanced above the Platyhelminthes in this respect, as well as in many others, but have not yet reached the point where a head as a morphologically distinct structure (as seen, for example, in Arthropoda) has become differentiated --- but they are nearer to this point than has been generally recognized.

CEPHALIZATION AMONG HELMINTH GROUPS OF UNCERTAIN POSITION

The Rotifera have little to offer from our present viewpoint. They tend to be bilateral but in habits are partially sessil. The mouth is always anterior and special sense organs (a tentacle and pigmented eye-spots) are sometimes developed at the anterior. The anterior always goes ahead in progression. The anterior is very sensitive to touch and selective as to food.

The latter point was determined by a simple experiment as follows: A large rotifer (Philodina sp.) was attached to a slide and feeding. I introduced carmine into the water in front of the animal. Soon, a steady stream of carmine grains was being brought against the trochal disc of the animal. These were all shunted down the side of the animal's body. Later, as more and more carmine came, the rotifer contracted, swung to one side, and then expanded again. The carmine induced this reaction quicker next time. After the rotifer had "tried" several directions and still the carmine came, it contracted immediately each time when struck by the carmine particles. Finally, it swam away to a region of less carmine where it immediately expanded its trochal disc and began to feed normally. Examination showed that, although thousands of carmine particles had come against the trochal disc, but few had been taken into the mastax. Prior to the introduction of the carmine and later, when the animal had

left the region of much carmine, bacteria and other particles could be seen entering the mouth of the animal in a steady stream. That the carmine did not enter, under the same circumstances, indicates selection of food; and this could only be accomplished by a sensitive anterior end, capable of being aware (in some sense, at least) that the carmine particles were not of the same nature as the bacteria. This does not, of course, predicate a conscious selection on the part of so simple an animal as this.

Gordiacea, Kinorhyncha, Gastrotricha, Chaetognatha, and Phoronida all show some cephalization. They have developed distinct anterior and posterior ends and many of them are more sensitive anteriorly than elsewhere.

The Acanthocephala are so degenerately specialized that one sees little tendency in this direction.

The Bryozoa are much like other sessil forms. While there is a tendency toward bilateral symmetry, there is also a tendency toward a radiate condition. This is superficially evident in the fact that many of them suggest coelenterate polyps when first seen.

Brachiopoda are essentially similar in these respects. Strictly speaking, they are bilateral but their sessil habits and peculiar feeding mechanism (the oral arms or lophophore) have precluded the development of a true head.

None of these minor groups show us any new tendency toward cephalization. They are, from our viewpoint, rather unimportant forms.

CEPHALIZATION AMONG ANNELIDA

The annelid worms show some very interesting things about cephalization. Standing as they do intermediate between the lower invertebrates and the higher, on the one hand, and between the aquatic and terrestrial invertebrates, on the other, they illustrate many biological principles very well. Among these is cephalization. Concerning this they show, too, the influence of an active life on the development of the head.

Among the Oligochaeta, Lumbricus may be taken as in many ways typical of the Megadrili. This organism shows cephalization by manifestation of the following: (1) having strict bilateral symmetry; (2) having the anterior go ahead in progression; (3) having a sensitive anterior end; (4) having an anteriorly placed mouth; (5) having nerve centers which tend to be larger at the anterior; and (6) having a tendency for regeneration to take place more readily and completely at the anterior --indicating a possible difference in metabolic rate. No sense organs occur as such (although sense receptors are developed), the whole ectoderm having retained its primitive function of response to such stimuli as those of light, heat, mechanical shock, electric shock, and probably chemical changes in the surrounding medium as well. It is to be especially noted, however, that the anterior regions are more sensitive to stimulation by these means than are other portions of the body.

In contrast to the Megadrili, let us consider Nereis, a genus of the almost wholly marine Polychaeta. This worm manifests cephalization in all of the ways listed above for Lumbricus and, in addition, has developed on its anterior region (1) two pairs of simple eyes, (2) a pair of prostomial tentacles, (3) four pairs of peristomial tentacles, and (4) a pair of sensory oral palpi. The mouth and pharynx are much more developed than those of Lumbricus, the former having tiny teeth known as denticles and a pair of very well-developed jaws, the latter having differentiated into a well defined introvert used for the procuring of food. Other Errantia are generally similar to Nereis in that they nearly all have a well defined head, a comparatively large cephalic nerve center, well developed sense organs, and a mouth and pharynx especially well differentiated.

Among the Tubicola, all sorts of conditions are to be found. Fundamentally they are much like the Errantia, often possessing eyes and, almost invariably, possessing tentacles of some sort. But the sedentary life secondarily adopted by most of them has given rise to all sorts of peculiar modifications in specific instances. All show some cephalization, however.

Now if we compare Lumbricus and Nereis as typically representative of their respective groups, we notice an interesting thing. The former is less specialized in those things which deal directly with the outside environment --- and therefore shows less cephalization. Sensory receptors

and nerve centers are not nearly so well developped. On the other hand (although this is somewhat aside from our present subject) should we compare these two annelids as to the organs dealing more directly with internal functions, such as those of reproduction, circulation, excretion, and digestion (as opposed to ingestion), we should find the reverse to be true; Lumbricus is, in these respects, more highly developed than Nereis.

The explanation of these differences is to be sought in the different habits and habitats of the animals. All of the Polychaeta are aquatic and all but a few marine. Those which show cephalization best (Nereis and other Errantia) are carnivorous, predatory, and typically free-swimming. The Megadrili are all subterrestrial, as is Lumbricus, and feed upon plants, leaf-mould, and similar substances for the most part. Living in the dark and eating plant materials which are abundant about them, the earthworms did not need to specialize the anterior end so much and therefore did not do so.

Another phenomenon which is exhibited by certain of the Polychaeta has a bearing upon our subject. Many of them reproduce asexually, forming thereby two (and occasionally more) types of individuals. These are known as atokes and epitokes. The former continue life such as is normal for their species, tending to hide away beneath rocks or among corals or seaweed. The latter are individuals especially specialized for sexual reproduction and live a brief life

swarming together at or near the surface of the sea where they shed their gametes and then die.

The chief interest to us in these phenomena is that the epitokes generally show a better cephalic development than other members of their species. Even Nereis, which shows but an incipient tendency toward this differentiation of sexual individuals, manifests something of the same thing in its heteronereis phase which has much larger eyes and a more differentiated cephalic region in general than unmodified individuals . The heterosyllis phase of Syllis manifests the same thing.

It seems that these special individuals, produced for a special function which happens to call for a more active existence, even though this is of brief duration, have developed a larger degree of cephalization than other members of their respective species. This is further proof that advancing cephalization is correlated with active habits of life.

The Microdrili are interesting in that they show a condition somewhere intermediate between the Megadrili and the Errantia. They are aquatic which accounts for many superficial resemblances to the Polychaeta, such as, for example, possession of eyes, and, especially, of longer and more specialized setae in several instances.

The Hirudinea are much like the Megadrili from our present point of view; on the whole, they show about the same degree of cephalic development as these.

The Sipunculoidea, in fact the whole Gephyrea, are

so specialized for a life beneath the sea bottom as to be somewhat exceptional annelids, if, indeed, they should be considered annelids at all. The anterior end in most of them (e.g., Phascolosoma and Sipunculus) is modified greatly to accommodate the very extensive introvert, used both in locomotion and in feeding. Cephalization is shown by these forms to some extent principally through bilateral symmetry and a differentiated anterior end. Sense organs and nerve centers are rather poorly developed, however, so that these animals do not show the degree of cephalization so characteristic of the marine Chaetopoda.

The reason for this is found in their habitat beneath the ocean floor and in their food habits. They belong to the great group of sand eaters to which also several groups of echinoderms belong. We shall see later how this habitat and these food habits have modified some of these latter (e.g., Synapta) so that they very closely resemble the Gephyrea. This is a case of convergent evolution in two radically different groups in adaptive response to similar habits and habitat. Many examples of this are to be seen among both animals and plants. Such a habitat tends to develop an elongate, bilateral body with a specialized anterior end but it also tends to suppress the development of organs of special sense and of nervous organization generally.

Concerning the annelid worms as a whole, we see that all show some cephalization. This is less marked in the semisedentary members of the phylum and in those specialized

for life below the earth's surface whether covered by the sea or not. It is most marked, as might be expected, in free-swimming and predatory forms.

SUGGESTIONS OF CEPHALIZATION IN ECHINODERMATA

The typical adult echinoderm is radiate in organization. A starfish, for example, carries any ray or rays ahead in progression. Its few primitive sense organs are located at the ends of the rays and the only thing which it has in the way of a special nerve center is the circumoesophegeal nerve ring which has been shown to have a coördinating function in the movement of the tube-feet. All of the Asteroidea, Echinoidea, Ophiuroidea, and Pelmatozoa (both recent and fossil) are essentially alike in these respects, although some, of course, have respiratory podia rather than tube-feet and there are many differences in details of structure. Therefore all of these manifest no cephalization.

But, curiously enough, all of these have bilateral larvae. This is interesting to us from two viewpoints, each closely related to our subject. (1) It may indicate that bilateral symmetry is more primitive than the radiate type. (2) It also serves as another illustration that an active life is correlated with bilaterality; for the echinoderm larvae are all free-swimming and pelagic --- typically much more active than their adults. Concerning the first of these, more needs to be said.

From our earlier discussion of the Protozoa, it might

have been inferred that I consider radiate organization more primitive than bilateral. It certainly is to be found most frequently in the more primitive animals. Yet, echinoderm larvae are bilateral whereas their adults are radiate, as stated above. How may one explain this?

Theoretically, there are three possibilities as to which of the two main types of symmetry is more primitive: either (1) the radiate type is; (2) the bilateral type is; or (3) neither is, each having arisen separately in the phylogenetic development of different groups of animals.

Which of these possibilities best expresses the facts, no one can certainly say. Were it not for the bilateral condition of larval echinoderms, the great preponderance of evidence would, as far as animals are concerned, favor the first, since radiate animals are always primitive and lowly creatures as compared with the more active bilateral forms. But, looked at from the broad viewpoint of general biology, the condition of the higher plants would still give us pause, for they are all of radiate organization and all are quite specialized.

This brings us back once more to the relation of symmetry to a sedentary life. Taking the organisms, both plants and animals, as we find them, the evidence seems most to favor the last possibility given above. Radiate organization probably arose separately in the various groups of both plants and animals which, early in phylogeny of each group, adopted or tended to adopt a sedentary existence. Bilateral

symmetry probably similarly arose in these forms which, in their early evolutionary development, tended to become active. Under this interpretation, we can understand why radiate animals have remained primitive, especially in respect to cephalization and nervous development generally, and also why the higher plants have done likewise; for it is a well established biological principle that, other things being equal, the greater the variety of environmental influences to which any given organism is subjected, the faster and more diversified will be its evolution. This is so provided only that the environmental conditions do not become so severe that the animal type in question be eliminated in the struggle for existence.

This is getting dangerously close to the old controversy of La Marckian evolution as opposed to Darwinism or De Vriesian mutation which has never been satistactorily settled. But it is not necessary to take a stand for one of these evolutionary theories to accept the theory that neither one of the two main types of symmetry is more primitive than the other. Whether the environment directly modifies the heredity of an organism (La Marckianism), merely selects from natural small variations which have survival value (Darwinism), selects from relatively large variations (De Vriesism), or whether any two or all three of these be true does not effect the general theory. The result postulated by the theory presented here theoretically could have come about in any of these manners.

Further evidence that the symmetry of animals had a dual origin is to be found in some of the adult echinoderms, notably in the Clypeastroidea, Spatangoidea, and Holothuroidea. All of these are sand eaters and all move about, more or less, below the surface of the ocean floor or lie partly buried in it. Belonging to a race generally primitive and radiate, they have, in adaptive response to a new environment, tended to become elongate and modified toward bilaterality. This can best be interpreted to mean that their early ancesters were wholly radiate but took on some of the habits characteristic of active forms. This has, in some manner and in some degree, tended to modify their evolution so that they now have a superficial bilateral symmetry superimposed upon a still radiate body.

The modification of the radiate form just mentioned is manifested in three different ways; (1) in a shifting of the position of the mouth and anus; (2) in an overdevelopment of certain of the petaloid areas; and (3) in various degrees of the modification of the test, especially by its elongation or flattening or both.

In Pygastrides relictus, a Caribbean protoclypeastroidean, the petals are wanting and the test is little modified. The anus, however, has shifted slightly its position at the aboral pole. In Echinarachnius parma, the petals are of equal size, the test little modified except for the typical flattening but the anus has migrated downward to the edge of the test. The mouth has retained its primitive position in the

center of the oral surface. Mellita is essentially similar in these respects to Echinarachnius except that the petals are larger on the surface opposite to that through which the anus opens. In Spatangus (Spatangoidea) the mouth has also shifted position --- this in the direction exactly opposite to the anus --- the petals are more differentiated on the area above the mouth, the test has elongated slightly on the axis containing the mouth and anus, and the whole test has become more depressed in the region above the oral aperture. Spatangus, therefore, suggests the protozoon, Centropyxis, earlier discussed.

These changes indicate a progressive cephalization in these radiate animals, culminating in the Spatangoidea which have a longitudinal axis, one end of which, that containing the mouth, goes ahead in progression; and the anus lies, in these forms, at the opposite end of this axis, exactly as it tends to do in typically active bilateral forms.

In the Holothuroidea we see the same tendencies but expressed in a different manner. Here, the lengthening of the body to form a longitudinal axis has been at right angles to the developing axis of the Spatangoidea and related forms. The oral opening and anus have retained their primitive positions and the whole body has become elongated oral-aborally. This makes the "anterior" of these animals to lie at the oral end, the "posterior" at the aboral. In many of them (e.g., Cucumaria and Thyone) the ambulacral areas have become larger on one side which tends to be carried downward. This

suggests a developing ventral surface. Synapta has lost all of its podia (save those about the mouth) and , as mentioned earlier, has become so elongated as very clearly to suggest a gephyrean. MacBride[2] makes mention of this resemblance in the following amusing fashion:

> "----- and taking into consideration the general superficial likeness of the two groups, the epigram is almost justified that 'if the Synaptida were not extremely careful they would become Gephyrea'".

CEPHALIZATION AMONG THE MOLLUSCA

All of the molluscs are bilateral and many species of them show quite a degree of cephalic development. The simplest (and probably the most primitive) in this respect are the various lamellibranchs, second come the scaphopods and amphineurans, third, the gastropods, and last, the cephalopods.

The sedentary or semisedentary lamellibranchs (e.g., Ostrea, Mytilus, Mya, Venus, Unio, Cardium, etc.) never have a head, however, in any true sense. In fact, many of them stand in the mud or sand with the posterior end upward and carry the dorsal or ventral surface ahead in what little progressive movement they make. The posterior end, associated with the all-important syphons, has, in most of them, especially in marine species, become more differentiated than the

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2 Cambridge Natural History, Vol. 1, p.577.

anterior. This is evident from the popular designation of the typical marine clam's fused syphons as the "neck of the clam".

Pecten is somewhat exceptional in having rows of simple eyes along the ventral portions of the pallium. The distribution of these indicates, however, little cephalization.

Typical lamellibranchs have sensitive ciliated palpi immediately associated with the mouth which serve to select food from the particles brought in by the water current flowing through the mantle cavity. These sense organs near the mouth may indicate a very slight tendency toward cephalization.

The Amphineura have a fairly well-developed head in which are located differentiated ganglia. From these, nerve cords pass to the body. Cephalization is thus manifested in a comparatively slight degree.

In the gastropods, a well-developed head is the rule, with tentacles, eyes, and mouth clearly associated therewith. Furthermore, several very large ganglia in or near the head serve as a principal nerve center, thus tending toward the development of a true brain.

In cephalopods, the head is better developed than in any invertebrate group except the arthropods --- but in a rather exceptional fashion. This needs further discussion.

The phylum Mollusca is supposed to have descended from a hypothetical primitive ancester, superficially somewhat like

the present-day amphineuran. This animal was bilaterally symmetrical and had a dorsal shell, a ventral foot, and a relatively straight intestine which ran from an anteriorly placed mouth to a posteriorly placed anus.

All of the classes of the phylum are supposed to have arisen from this ancestor through (1) the humping of the back to accommodate more organs and a more coiled intestine (forming a visceral mass or hump); (2) the modification of the shell; and, especially, (3) the modification of the foot to serve various functions. These great changes were, of course, associated with a host of minor and secondary modifications resulting from them or associated with them.

Concerning the phylogenetic modification of the molluscan foot there are phenomena of great interest from our present viewpoint. The lamellibranchs developed the original flat foot into the typical hatchet-shaped structure so characteristic of them. The Amphineura and Gastropoda retained essentially the primitive condition. The Scaphopoda developed a peculiarly specialized structure used, together with the cone-shaped shell, for burrowing in the ocean floor.

In the early cephalopods, the shell was greatly developed but, with the assumption of a free-swimming existence, correlated with carnivorous food habits, this structure has tended to be lost. Small internal shells still exist among the squids but the octopi have lost them altogether.

Correlated with the reduction of the shell and the development of free-swimming habits, the cephalopdian foot

tended to become split into many arms (eight in octopi, ten in squids, and many in nautli). Each arm typically developed suckers, the better to attack fishes, Crustacea, and other animals used for food and to serve, in case of danger, as a defensive weapon.

Thus, the function of the foot has changed from that of a simple, muscular organ of locomotion to that of an organ of offense, of defense, and of feeding.

The development of free-swimming habits in the cephalopods is correlated also with the lengthening of the body. This is readily seen if we compare an octopus, which has a relatively short body, with a typical squid like Loligo or Sepia whose body is shaped like a dart or arrow. While octopi can and do swim, they are not nearly so active as are the squids, spending most of their time in caves or among rocks. The squids, on the other hand, actively hunt fishes and other quick creatures for food and are very nicely coördinated and graceful in movement.

A carnivorous animal must of necessity have quickness and sureness of movement in order to capture prey; it must have well-developed sense organs, too, in order that it may the better find its food and the better avoid its own enemies. The response of such an animal to such habits furthers cephalization; and, conversely, advance in cephalization fits the animal to such habits.

Accordingly, the cephalopods have developed beyond most other invertebrates in cephalization, as was earlier said.

The head, in these forms (especially in Dibranchiata), is a distinct morphological structure. It contains large nerve centers which collectively form almost a brain. The mouth is differentiated for the tearing of prey, being armed with a horny, curved beak suggestive of that of a parrot or hawk except that its lower jaw is typically larger than the upper. The eyes are very large, built upon the same fumdamental plan as those of vertebrates, and are thought to be functionally just as effecient.

Now, if we look a little more closely at the fundamental primitive plan of molluscan structure as exemplified by the hypothetical ancester of the group earlier mentioned and attempt to see just how its structure was modified in the development of recent cephalopods, we see a very interesting thing. The shell was reduced, the body was lengthened, the foot was split into several arms, and the mouth became associated more nearly with the ventral surface and, therefore, with the foot. The mantle became more muscular and gradually lost its primitive secretory function in favor of that of locomotion. The foot, accordingly, lost its primitive locomotor function and became a well-differentiated organ of offence, defense, and feeding, as earlier mantioned. These shiftings of relationships and functions of parts, coupled with the assumption of free-swimming and predatory habits, became associated with the lengthening of the body. Since the mouth was now associated with the ventral surface and the foot with the mouth, it became of advantage for the ven-

tral surface to go ahead in progression. And this surface, therefore, rather than the anterior end, tended to develop the principal nerve centers and sense organs --- that is, it took on more and more the function of an anterior end.

Thus it came about that the cephalization so greatly developed in the Cephalopoda came to be associated with the ventral surface. The head actually developed on this surface and the elongating of the body was along the dorso-ventral rather than along the longitudinal axis. The apparent anterior of a squid is, therefore, in reality a cephalized ventral; the opposite, apparently caudal, is the true dorsal.

It is interesting to note that in octopi the body did not lengthen so much as in squids; and these animals still use the foot for locomotion to some extent. It is also to be remembered that they are not so active as squids. In respect to cephalization, therefore, the squids are more specialized than octopi: in some other respects (e.g., in the reduction of the shell) they are more primitive.

It should, perhaps, be noted that the interpretation of cephalopodian structure given above is not completely accepted by all zoologists. That it generally is by most authorities, however, is indicated by the almost universally used name for the group, Cephalopoda, which means "head-footed".

Taking the Mollusca as a whole, we may summerize the manifestation of cephalization among them as follows: the inactive lamellibranchs show it little; the slow-moving gastro-

pods, Amphineura, and scaphopods show somewhat more; the active cephalopods have it to a marked degree. The last, however, have developed the head on the ventral surface: and the more active they are, the more has the head developed. Shell-bearing forms among the Cephalopoda have largely lost out in the race for life: formerly very numerous, they are now represented by the single genus, Nautilus, with but few species inhabiting the warm waters of tropical and subtropical seas.

CEPHALIZATION AMONG THE ARTHROPODA

The Arthropoda have little new to offer to our discussion. Examination of them shows indications of the highest degree of cephalization attained by any invertebrate group. All of the characteristics listed earlier as indicative of cephalic development are shown in high degree and true auditory organs are developed in many terrestrial members of the group for the first time in the animal series.

Little would be gained from our viewpoint by a detailed discussion of the complexity of the arthropods' sense organs (such as the compound eyes; organs of balance, of taste, of smell, and of other chemical sense located on the antennae or in the mouth; or auditory organs, either associated with the head or on the legs or thorax, the latter as in some of the Orthoptera). Similarly, little value would be added to our account by detailed discussion of the differentiation of appendages used as mouth parts (e.g., maxillae, maxillipeds, and mandibles of decapod Crustacea or the mandibulate or suc-

torial mouth parts of insects). All of these and similar characters indicate a high degree of cephalization --- but they show little that is new to us as to how it developed.

It is to be noted, however, that here, as elsewhere, cephalization is best developed in the most active forms. A few parasites (e.g., among the copepods and Linguatulida) have tended to lose the head as a result of parasitic degeneration. Similarly, insect larvae whose parents care for their welfare (e.g., Apidae, Vespidae, and others) have little cephalization. Where parental care is not developed, however, and the young have to shift for themselves, heads with well-developed sense organs are the rule (e.g., hellgramites, most larval beetles, dragon-fly larvae, etc.). In most of the former cases, the head has probably degenerated, i.e., lack of cephalization here is not a primitive characteristic.

Arthropods are among the most successful of animals -- in many respects the most successful of all. It is quite likely that their great cephalic development has been a major factor in this, since the only animals which rival them here are the vertebrates; and the latter are the highest organisms in existence in cephalization. That cephalization is not the sole factor in biological success, however, is indicated by the condition among the Mollusca already discussed. There are many more arthropods than cephalopods; but there are many more lamellibranchs and gastropods also, both of which, as indicated earlier, are below the cephalopods in cephalization.

SUMMARY

1. Cephalization is defined as the phylogenetic development of a head or a tendency toward such development.

2. Beginnings of cephalization are indicated by any one or by any combination of the following characteristics: (1) possession of bilateral symmetry or a tendency toward it; (2) having one end of the body more sensitive than other parts; (3) possessing a metabolic gradient; (4) having special sense organs localized toward one end of the body; (5) having the mouth at one end; (6) having a tendency to mass nerve centers at one end of the body; and (7) having a tendency to carry one end ahead in progression, especially the one containing the mouth, nerve centers, and sense organs.

3. Protozoa show various conditions of cephalization. None have a distinct head. Amoebina show a very weak tendency toward cephalization; Testacea show from none (in Arcella) to a weak beginning in Centropyxis and Difflugia; Heliozoa, Radiolaria, and Foraminifera show no cephalization. Mastigophora show more cephalization than Sarcodina; this is mainly by having (1) a stigma (absent in some), (2) a mouth at one end (although non-functional in most pigmented forms), and (3) a tendency to carry one end ahead in locomotion. Sporozoa show little tendency toward cephalization. Infusoria show several conditions: Suctoria have little or no cephalization as adults, Ciliata vary

among the orders: Holotricha have anterior and posterior ends and usually show some differentiation of dorsal from ventral (although there are exceptions); Hypotricha have in addition right and left sides; Peritricha and Heterotricha are sometimes radiate forms which show some cephalization when free-swimming; Oligotricha vary among themselves, some showing slight degrees of cephalization, others prcatically none.

4. Porifera show no cephalization as adults; their larvae suggest holotrichous ciliates in this respect.
5. Coelenterata have sensitive oral surfaces (especially in polyps); some have a metabolic gradient. This is their only manifestation of cephalization.
6. Ctenophora show a tendency toward bilateral symmetry; otherwise they resemble Coelenterata.
7. Platyhelminthes show the first true cephalization in the animal series. This is shown by practically all of the tests for cephalic development given above, in (2). In Cestoda, however, cephalization is weak due to degenerate specialization.
8. Nematoda show cephalization to a marked degree although morphologically distinct heads are rare. These worms are much more specialized, in many respects, than is commonly supposed.
9. All other free-living types among the lower worm-like animals show some degree of cephalization, although this slight in sessil forms. Of these, Molluscoidea probably

show the least.

10. Annelida show cephalization in various degrees depending upon habits and habitat of individual types. Polychaeta, although generally considered more primitive in general than Oligochaeta, are more specialized in this respect. Hirudinea are slightly more cephalized than Megadrili and about the same as Microdrili.

11. Typical echinoderms are radiate forms and show no cephalization as adults; their larvae are bilaterally symmetrical. Three groups (Clypeastroidea, Spatangoidea, and Holothuroidea) have joined the sand eaters and have taken on various degrees of bilateral symmetry in consequence; in this they show weak cephalization.

12. Mollusca vary in cephalization with the habits of the classes: Lamellibranchiata are sedentary (or semi-sedentary) and have little; Gastropoda, Amphineura, and Scaphopoda are slow-moving and show more; Cephalopoda are very active and predatory and have very marked cephalization. The last have the ventral rather than the anterior specialized as the head. No group illustrates so well the principle that an active life furthers cephalization and that a sessil life tents to suppress it.

13. Arthropoda show the greatest cephalic development to be found among invertebrates. Degenerate parasites among them and the larvae of some of the higher insects have lost the head through degeneration in response to special habits. The great biological success of arthropods is probably cor-

related with their great cephalic development.

CONCLUSIONS

We have traced the broad outlines of the phylogenetic development of the head (or a tendency for this development) among the various important invertebrate phyla. From the facts presented we may draw the following conclusions:

1. Cephalization in an incipient form is found low down in the animal kingdom.
2. The first true cephalization is found among the lower Platyhelminthes.
3. Cephalization is definitely correlated with the development of bilateral symmetry.
4. Cephalization is most developed in active forms, especially in those of predatory habits.
5. Animal types whose ancestors were active and bilateral and which manifested cephalization tend to have the head degenerated if they have secondarily adopted a sedentary or endozoic existence.
6. Cephalization is probably one of the major factors in the biological success of bilateral animals, especially among the higher types; the insects illustrate this tendency better than other invertebrates.
7. The most interesting and important invertebrate phyla from the viewpoint of cephalization are the Protozoa, Platyhelminthes, Annelida, Echinodermata, and Mollusca.

These conclusions may be taken as tentative and sub-

ject to possible change. We are dealing here with all of the perplexing problems of phylogeny, taxonomy, and general evolution concerning which very little is accurately known. It would not be surprizing, therefore, if others having knowledge equal to or greater than mine should put different interpretations on some of these facts. The whole subject is, in the nature of things, speculative. What is needed now is to test these conclusions by observation and critical experimentation and to modify them in any way necessary in accordance with any valid results obtained.

BIBLIOGRAPHY

1. Berry, Ed. W.; Cephalopod Adaptations --- a Record and its Interpretation; 1928, Quart. Rev. Biol., Vol. 3, pp. 92-107.

2. Borradaile, L. A., and Potts, F.A.; The Invertebrata; 1932, Camb. Univ. Press.

3. Bragg, A. N.; Invertebrate Zoology, 1933, (in manuscript).

4. Brooks, W. K.; The Affinity of the Mollusca and the Molluscoidea; 1876, Proc. Bost. Soc. Nat. Hist., Vol. 18, pp.1-11.

5. -----, -,-; The Foundations of Zoology; 1915, 2nd. ed., Columbia Univ. Press.

6. -----, -, -; The Oyster; 1905, 2nd. ed., The Johns Hopkins Press.

7. Calkins, G. N.; Biology of the Protozoa; 1926, Lea and Febiger, Phila.

8. Cobb, N. A.; Free Living Nematodes; in Ward and Whipple's Fresh Water Biology, 1918, p. 459; Wiley, N. Y. C.

9. Coe, W.R.; The Echinoderms of Connecticut; 1912, Bul. 19, State Geol. and Nat. Hist. Sur., Hartford.

10. Chandler, A. A.; Introduction to Human Parasitology; 1929, Wiley, N. Y. C.

11. Delage, Y., and Hérouard, E.; Traité de Zoologie Concréte; 1899, Reinwald, Paris.

12. Ferris, G. F.; The Principles of Systematic Entomology; 1923, Univ. of Chicago Press.

13. Kudo, R. R.; Handbook of Protozoology; 1931, Thomas, Springfield, Ill.

14. Lankaster, E. Ray (and others); A Tretise on Zoology; from 1900, Black, London.

15. MacBride, E. W.; Textbook of Embryology, Vol. 1; 1914, Macmillan, London.

16. -------, -,-., (and others); The Cambridge Natural History, Vols. 1-8; from 1909, Macmillan, London.

17. Minchin, E. A.; An Introduction to the Study of the Protozoa; 1922, Arnold, London.

18. Myers, F. J.; The Rotifer Fauna of Wisconsin V, The Genera Euchlanis and Monommata;1930, Trans. Wis. Acad. Sci. Arts and Letters, Vol. 25, pp. 353-409.

19. Parker, T. J., and Haswell, W. A.; Textbook of Zoology, Vol. 1; 1914, Macmillan, London.

20. Pearce, A. S.; The Migration from the Ocean into Fresh Water and Land Habitats; 1927, Am. Nat., Vol. 61, p. 466.

21. -----, -. -; Observations on the Fauna of the Rock Beaches at Nahant, Mass.; 1913, Bul.Wis. Nat. Hist. Soc., Vol. 11 (n. s.) and continued, ibidem, 1914, Vol. 12.

22. Richards, Aute; Outline of Comparative Embryology; 1931, Wiley, N. Y. C.

23. Rodgers, C. G.; Textbook of Comparative Physiology; 1927, McGraw-Hill, N. Y. C.

24. Stafford, Jos.; The Canadian Oyster; 1913, Commission of

Conservation of Canada, Ottawa.

25. Tait, John; Homology, Analogy, and Plasis; 1928, Quart. Rev. Biol., Vol.3, pp. 151-173.

26. Woodward, B. B.; The Life of the Mollusca; 1913, Methuen, and Co., London.

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